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Influence of age on reproductive performance in the Seychelles warbler

Jan Komdeur
Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK, and National Environmental Research Institute, Department of Wildlife Ecology, Kalö, Grenåvej 12, DK-8410 Rönde, Denmark

I studied age-related breeding performance of the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) on Cousin Island, Seychelles, during 14 years. The annual number of young that fledged is significantly related to territory quality and number of helpers in the breeding group. Accounting for these factors and for the partner's breeding experience, annual production of fledglings by breeding birds increases from 2 to 5 years and decreases beyond 5 years of age. Age-related changes in reproductive success within breeding individuals, paired with the same experienced partner and occupying the same breeding territory with similar amount of food from 2 to 8 years of age, show that Seychelles warblers have higher hatching success and produce more hatchlings and fledglings as they become older. This is probably not a response to decreasing residual reproductive value caused by decreasing life expectancy as they become older. Primiparous warblers produce the same number of fledglings as multiparous warblers of the same age, have a similar life expectancy as multiparous warblers, and occupy territories with similar amounts of resources available for reproduction. As all warblers have similar access to food before reproduction and similar foraging efficiency, the low reproductive success in younger warblers cannot be ascribed to differences in environment but to the bird's ability to breed successfully (e.g., a result of previous helping and/or breeding experience). Effects of senescence on reproduction begin to occur from age 6 for both sexes. From that age, eggs have lower hatching success, but fledging success remains the same. Birds that start breeding at a young age on a given quality territory produce more fledglings in their lifetime than birds that delay breeding. Many old birds never fledge young of their own. They have not been able to breed because of a shortage of breeding territory vacancies. *Key words:* age, cooperative breeding, reproductive success, senescence, Seychelles warbler. *[Behav Ecol 7:417–425 (1996)]*

Age-specific reproductive success has been observed in many bird species (Clutton-Brock, 1988; Forslund and Pärt, 1995; Newton, 1989; Newton et al., 1981; Nisbet et al., 1984; Nol and Smith, 1987; Partridge, 1989; Perrins and McCleery, 1985; Sæther, 1990). An understanding of how age influences breeding success is important to studies of life history evolution and population demography (Clutton-Brock, 1988). Our insight in the causes of variation in breeding success with age is, however, limited. Two mechanisms have been proposed to explain age-specific differences in reproductive performance. First, individual reproductive success may improve with age because of age-related improvements, such as in foraging efficiency, or because of accumulated experience (Coulson and Horobin, 1976; Forslund and Pärt, 1995; Newton, 1989; Newton et al., 1981; Nol and Smith, 1987; Perrins, 1979). The crucial experience consists of learning and/or practicing the skills associated with nest-building and caring for eggs and young. Second, reproductive success may change with age because of senescence, the tendency for aspects of performance such as survival and fertility to decline with advancing age (Partridge, 1989).

Age-dependent reproduction is not easy to record accurately (Newton, 1989): (1) Most studies of recognizable individuals have lasted less than the lifetimes of the birds concerned; (2) there might be inevitable gaps in breeding records, because it is difficult to keep track of a large number of individuals throughout their breeding lives (viz. change to unknown breeding localities during their lives); (3) not all individuals reach the senescent phase, as death occurs at all stages and only a minority of individuals reach old age; and (4) studies on age-specific differences in reproductive performance frequently have not separated the effects of age from those of other confounding variables. Studies on reproduction have only recently started to examine relationships between parental age and fecundity while simultaneously controlling for likely confounding variables (Clutton-Brock, 1988; Newton, 1989).

In this paper, I report on the relationships between age and reproductive performance of the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). The species is a rare island endemic, until 1988 known only from Cousin Island (29 ha) in the Seychelles. The most common clutch size is a single egg (91.0%, n = 223). Although warblers can breed successfully in their first year, some individuals remain on their natal territories as helpers and do not breed for several years, sometimes throughout their life (Komdeur, 1992). Helpers aid in territory defence, predator mobbing, nest-building (mainly females), incubation (females only), nest-guarding (mainly males) and feeding of dependent young which that probably are not genetically their offspring (Komdeur, 1994a). Young birds are more likely to stay on good quality territories, because of higher foraging success leading to increased survival (Komdeur, 1991). Most of these young become helpers leading to higher reproductive success of their parents and hence, higher indirect fitness benefits for the helper (Komdeur, 1992; Komdeur et al., 1995), which was confirmed by removal experiments of helpers (Komdeur, 1994a).

Using both cross-sectional and longitudinal data, I examine the extent to which variation in reproductive performance is caused by differences among individuals or by changes within

J. Komdeur is now at: Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia.

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individuals as they age. I use 14 years of data from an individually marked and genealogically known population. During a 10-year period, I have been able to record every nesting attempt and its success for all individual warblers. For some individuals breeding performance is exactly known throughout their breeding lives. As warblers survive better in richer territories, then supposed "reproductive improvements with age" may be simply a reflection of different territory qualities occupied by different-aged birds. Breeding success of the breeding pair could also be enhanced by the presence and the sex of helpers, because of the sex-specific tasks. The experience of the breeder's mate could affect reproduction (e.g., the more experienced the birds are in breeding, the higher the breeding success). In the analyses, I accounted for the effects of age, experience of breeding partner, presence of helpers, and territory quality.

METHODS

Data collection

The entire population of Seychelles warblers on Cousin (115–123 groups, 310–400 birds) was under continuous study between January 1981 and July 1994. For each breeding bird of known age (color-ringed as nestlings) detailed data were available on annual number of young fledged per year and mean yearly group composition. From 1985 on, I checked all territories biweekly for active nests and cooperative breeding. For each nesting attempt, I recorded the identity of breeders, the identity (and number) of helpers, the clutch size, and number of young successfully fledged and reaching independence. The young are fed by their parents and helpers for up to 3 months (Komdeur, 1991). Hence, I considered them to have reached independence at the end of this period. Observations on nest-building were conducted in the second week after nest initiations. Observations on incubating, nest-guarding (when the bird was less than 2.5 m from the nest) were conducted in the second week after egg-laying. Food provisioning observations started two weeks after hatching and were repeated every three weeks until the young died or reached independence. Each observation period comprized three 1-hour segments in periods equally spaced during the day: 0630–1030, 1030–1430 and 1430–1830 hours. At every half minute I recorded whether a bird was engaged in any of the above mentioned behaviors. Each territory was checked fortnightly for the presence of color-ringed birds to determine the proportion of birds that died or survived. Once a bird was missing from its territory, all other territories were checked to assess dispersal. As emigration from the island never occurred, I assumed that missing birds had died.

To test whether age of the bird affected foraging success, each year intensive foraging studies were conducted in May, just before the breeding season, on non-moulting and non-breeding adult warblers. For 285 adult warblers foraging observations were taken during a 30-minute-period. At half-minute intervals it was noted whether or not foraging had taken place. During foraging, the first prey item taken, number of pecks, and the number of successful and non-successful pecks were recorded during the half-minute interval. The warblers were remarkably tame and were observed from within a few meters, which enabled the scoring of prey types. A successful peck was one after which the bird was seen swallowing food. Foraging success was expressed as the mean number of successful pecks per half minute of foraging, and percentage foraging as the percentage of total time the warbler was seen foraging. Foraging efficiency was the product of foraging success and percentage of time spent foraging.

Territory quality

Territory quality could be measured in terms of availability of nest sites, density of predators, or food availability. Nest sites had no consistent features (within the same territory nests were found from 1 m to 20 m) and were abundant. Adult Seychelles warblers lack natural predators. Nest predation risks seemed to be the same on each territory, as nest predators [Seychelles fodies (*Foudia sechellarum*), which are weaver birds endemic to the Seychelles, and two endemic skinks (*Mabuya wrightti* and *Mabuya sechellensis*)], were evenly distributed over the island (Brooke and Houston, 1983; Komdeur, 1994b; Owen, 1986) and territories (Komdeur, 1991). Because the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur, 1991), the quality of a territory depends on the amount of insect prey available, which in turn depends on the amount of foliage present. Territory quality, *tq*, was measured as:

$$tq = a \sum_{x=1}^{12} (c_x i_x)$$

where a is mean annual territory size (ha), c_x is mean foliage cover for plant species x, and i_x is mean insect totals for plant species x per unit leaf area (1 dm^2) in the territory. The only other insect-eating birds on the island were the Seychelles fody and the endemic Seychelles sunbird (*Nectarinia dussumieri*).

The amount of foliage in each territory was measured using a transect method. The transect was 250 m long, subdivided into straight subtransects plotted 25 m apart from each other and facing north from one territory boundary to the other. Every 5 m the presence or absence of foliage and the plant species were noted in the following heights: 0–0.75 m, 0.76–2.0 m, 2.1–4.0 m, and at 2-m intervals thereafter. Total foliage cover for plant species x (c_x) was the total number of cases of presence of foliage at all heights along the transect. To assess prey availability, i_x, in each territory, the upper- and undersides of 50 leaves per plant species (12 dominant species) were searched for insects. Insect density was assessed for plant species by measuring the area of 250 leaves at 50 random sites on the island (five leaves per site).

I measured the quality of all territories each month. For some analyses territories were divided into two categories: low (tq = 0-1500) and high quality (tq > 1500).

Definitions of variables

Age: age (years) of the bird, based upon known hatching dates. *Reproductive success*: the number of fledglings produced. *Primiparous bird*: a bird breeding for the first time in life. *Multiparous bird*: a breeding bird that had bred in previous years. *Experienced bird*: a breeding bird that had fledged young in a previous year.

Data analyses

As the minimum age at first helping or breeding was 1 year (Komdeur, 1991), only data from birds older than 1 year were analyzed, and only helpers older than 1 year have been counted in "breeding" group size. However, analysis of mean age in relation to first reproduction was restricted to birds at least 5 years of age, to minimize the bias toward shorter-lived birds, which never bred. For birds older than 5 years that never produced young before dying, first reproduction was assumed to occur in the year of death, to minimize the underestimation of age at first breeding. Analysis of the influence of age at primiparity on reproductive performance by males and females was restricted to birds occupying low-quality territories

that were paired with an experienced partner and with no assistance from helpers. I did not include primiparae from high-quality territories, because on most (90.6%; $n = 53$) high-quality territories one or more additional adult birds were present, thereby affecting reproductive performance (Komdeur, 1994a).

Cross-sectional tests were based on one randomly selected age category for each breeding bird to avoid pseudoreplication; 356 bird-years during 1981–1994. Breeding records from all male and female individuals of each age class were pooled to see how breeding performance altered from one age class to another. The factors affecting reproductive success were analyzed by forward stepwise multiple regression, in which the first variable considered for entry into the equation is the one with the largest positive or negative correlation with the dependent variable. A variable enters into the equation only if the probability, p, associated with the F test is less than .05. I have tested the stability of the results from the stepwise regression. If the criterion is met, the variable is entered into the equation and the procedure is repeated. The procedure stops when no other variables meet the criterion.

Age-related changes of reproductive performance and foraging efficiency within individuals were investigated for eight consecutive years. I restricted within-individual analysis to 15 males and 17 females born in 1984–1986 that became breeders on low-quality territories in their second year, stayed in the same breeding territories and were paired with the same experienced partners during the whole period, and had never received assistance from helpers. Because cohorts were equally spread over the 3-year period (1984, 1985 and 1986: 5, 6, and 4 for males, and 7, 6, and 4 for females). I did not examine for cohort variation. It was necessary to exclude the older cohorts because each was represented by only a few individuals and to exclude the younger cohorts because their reproductive performance is not known yet for an 8-consecutive-year period. I did not include birds breeding on high quality territories for 8 consecutive years, because most individuals (91.7%; $n = 36$) had received assistance of a variable number of helpers during (part of) their reproductive life, leading to increased reproductive success. A multivariate analysis of variance designed for repeated measures (MANOVA) was applied to assess the effect of age on data on reproductive success and foraging efficiency. Repeated measures designs differ from ANOVAs in that the different levels of age cannot be randomly assigned to the age intervals.

Unless stated otherwise, means are expressed with standard errors, probability values are two-tailed, and the null hypothesis was rejected at $p < .05$.

RESULTS

Reproductive performance in relation to age at primiparity

The age of first breeding in the Seychelles warbler ranged from 14 months to 6 years. Some remained in their natal territory and did not breed at all. For example, one female stayed with her parents as a helper her whole life and died at 8 years. Mean age of first breeding was 3.2 years for females ($\pm$ 0.17, $n = 70$) and 3.0 years for males ($\pm$ 0.13, $n = 58$). The proportion of 2-, 3-, 4-, 5- and 6$^+$-year-olds that were breeding for the first time in life was 0.39 (30/78), 0.22 (11/50), 0.42 (20/48), 0.16 (4/25) and 0.11 (5/47), respectively, for females and 0.46 (26/56), 0.39 (11/28), 0.44 (19/43), 0.12 (2/17) and 0.00 (0/13), respectively, for males. Further analysis of the influence of age at primiparity on reproductive performance was restricted to 2-, 3- and 4-year-olds in view of the small sample size of the older age classes.

For any age class of male and female primiparae, annual number of nesting attempts, clutch size, and the proportion of hatchlings reaching independence were all similar (Table 1). Because there was no significant difference in the breeding performance of 3- and 4-year-old primiparae (Table 1), I combined these data and tested for differences with 2-year-old primiparae. In females, 2-year-old primiparae had a significantly lower probability of nests containing a clutch and lower hatching and fledging success than 3- and 4-year-old primiparae. As a consequence 2-year-old primiparae produced significantly fewer young; none of the hatchlings fledged successfully. In males, the proportion of nests containing a clutch, mean number of nests with clutch, and fledging success were independent of age at primiparity. In males, 2-year-old primiparae had a significantly lower hatching success than 3- and 4-year-old primiparae, and as a consequence produced fewer hatchlings, fledglings, and independent young. For both males and females, the probability of producing fledglings and the mean number of fledglings produced the next year were not associated with age at primiparity (Table 1). In addition, the production of fledglings over estimated lifetime was the same for 2- and 3-year-old primiparae but was significantly less for 4-year-old primiparae (Table 1). For any age class of male and female primiparae, foraging success and percentage time spent foraging were similar, as well as quality of the breeding territory (Table 1).

Factors affecting reproductive success

Reproductive output varied significantly with age of the Seychelles warbler (Figure 1A). For both males and females there was a clear increase in breeding success in the early years of life and a clear deterioration thereafter. In both sexes, no individuals bred successfully at age 1 and a few bred successfully at age 2. The fraction of older birds that had never fledged young of their own was quite large (Figure 2). By age 3, about half of the males had never fledged young, but by 5 years of age all males had fledged at least one offspring. At age 4, half of the females had never fledged young. Only by age 9 were most females likely to have fledged at least one offspring. When reproductive output records were pooled from breeding males and females (e.g., no delayed breeding), then reproduction increased quickly from 2 to 3 years of age, remained similar between 4 and 6 years of age, and decreased thereafter (Figure 1B). Overall reduced reproductive output in the early years of life was attributed to delayed breeding.

Table 2 lists the effects of factors, analyzed by means of forward multiple regression, that have been hypothesized to account for reproductive success of breeding Seychelles warblers. I have included the quadratic term of territory quality, as with increasing territory quality the reproductive success reaches a plateau (Komdeur, 1991). Overall, the annual number of young fledged was significantly related to territory quality, group size, gender, and age of the bird. Of these variables territory quality explained most of the variance. In the Seychelles warbler, the annual number of fledged young, controlling for group size and partner's breeding experience, showed significant differences both among age classes and territory quality classes (Figure 3). Medium-aged males and females breeding on a given quality territory performed significantly better than both younger and older birds. Male and female warblers occupying high-quality territories produced significantly more fledglings than even-aged warblers of low-quality territories. After controlling for territory quality, the size of the group significantly affected reproduction (Table 2). An individual's reproductive success thus depends on the quality of its territory as on the attributes of the breeding group. Also, the annual number of fledged young, controlling for territory quality and partner's breeding experience, was

Table 1

Annual breeding performance (SE) and foraging efficiency (SE) of Seychelles warblers on low-quality territories in relation to age at primiparity

	Age at primiparity (years)			*p*			
	2	3	4	3 versus 4	2 versus 3/4	2 versus 3	2/3 versus 4
Females							
Nest attempts	1.13 (0.14)	1.00 (0.00)	1.44 (0.27)	NS	NS		
Clutch/nest attempt	0.37	0.78	0.62	NS	.012*		
Nests with clutch	0.42 (0.10)	0.78 (0.15)	0.89 (0.00)	NS	.017		
Clutch size	1.0 (0.0	1.0 (0.0)	1.0 (0.0)	NS	NS		
Hatchlings/egg	0.30	0.86	0.75	NS	.012		
Nests with pulli	0.13 (0.07)	0.67 (0.17)	0.67 (0.18)	NS	<.001		
Fledglings/hatched egg	0.00	0.83	0.83	NS	.018		
Nests producing fledglings	0.00 (0.00)	0.56 (0.18)	0.56 (0.17)	NS	<.001		
Independent young/hatched egg	0.00	0.67	0.75	NS	NS		
Nests producing independent young	0.00 (0.00)	0.44 (0.18)	0.50 (0.17)	NS	<.001		
% Foraging	88.1 (8.9)	88.9 (10.5)	91.0 (7.9)	NS	NS		
Foraging success	2.12 (0.51)	2.08 (0.63)	2.17 (0.48)	NS	NS		
Territory quality	6.83 (4.01)	4.77 (3.05)	5.78 (3.46)	NS	NS		
n	24	9	18				
% Females producing fledglings next year (*n*)	62.5 (24)	55.6 (9)	83.3 (18)	NS	NS		
Fledglings next year/female	0.71 (0.11)	0.89 (0.11)	0.67 (0.14)	NS	NS		
Lifetime production of fledglings (SE, *n*)	2.50 (0.33, 14)	2.44 (0.81, 9)	1.28 (0.18, 18)	.001	—	NS	<.001
Males							
Nest attempts	0.90 (0.13)	1.00 (0.26)	1.41 (0.12)	NS	NS		
Clutch/nest attempt	0.82	0.83	0.92	NS	NS		
Nests with clutch	0 74 (0.10)	0.83 (0.17)	1.29 (0.14)	NS	NS		
Clutch size	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	NS	NS		
Hatchlings/egg	0.43	1.00	0.50	NS	.001		
Nests with pulli	0.32 (0.11)	0.83 (0.17)	0.65 (0.17)	NS	.044		
Fledglings/hatched egg	0.67	0.60	0.91	NS	NS		
Nests producing fledglings	0.21 (0.10)	0.50 (0.22)	0.59 (0.17)	NS	.044		
Independent young/hatched egg	0.50	0.60	0.82	NS	NS		
Nests producing independent young	0.16 (0.09)	0.50 (0.22)	0.53 (0.15)	NS	.022		
% Foraging	86.5 (8.8)	90.7 (3.7)	85.9 (8.1)	NS	NS		
Foraging success	2.13 (0.81)	2.08 (0.54)	2.40 (0.96)	NS	NS		
Territory quality	6.47 (2.93)	4.50 (2.99)	7.59 (4.49)	NS	NS		
n	19	6	17				
% Males producing fledglings next year (*n*)	55.5 (18)	50.0 (6)	68.8 (16)	NS	NS		
Fledglings next year/male	0.56 (0.12)	0.67 (0.21)	0.69 (0.15)	NS	NS		
Lifetime production of fledglings (SE, *n*)	2.88 (0.35, 16)	2.17 (0.17, 6)	1.27 (0.18, 15)	.018	—	NS	<.001

Statistical significance of comparisons determined by Fisher's exact tests (proportion and percentage data) or Mann-Whitney *U* test; NS = not significant. * Yates correction.

Lifetime production of fledglings is the number of fledglings produced during the first five years of life, which is the average adult life expectancy of warblers on low quality territories (Komdeur, 1992).

significantly affected by both the age of the breeding bird and the presence of helpers (Figure 4). In situations were helpers were absent or present, medium-aged male and female warblers had higher breeding success than younger or older birds. However, breeding birds that received assistance from helpers performed significantly better than breeding birds without assistance. After controlling for both territory quality and group size, gender had a significant effect on reproduction, and after controlling for gender, the age of the bird had a significant effect on reproduction (Table 2). The variables group composition (number of females and number of males) and year of study had no significant effect (Table 2). The annual number of fledged young, controlling for territory quality, group size, and partner's breeding experience, showed significant differences among age classes, both in breeding males and females (Figure 5). Once again, the general pattern was that medium age classes performed better than did younger and older birds. In males, reproduction increased quickly from 3 to 6 years of age and decreased significantly beyond 6 years, and in females reproduction increased from 2 to 5 years of age and decreased beyond 5 years of age.

Parental age and reproductive performance

Using longitudinal data, I investigated age-related changes in reproductive success within breeding males and females, paired with the same experienced partner and occupying the same low-quality breeding territories from 2 to 8 years of age (Table 3). Annual numbers of young reaching independence and 1 year of age were not included in this analysis because not all fledglings were color-ringed.

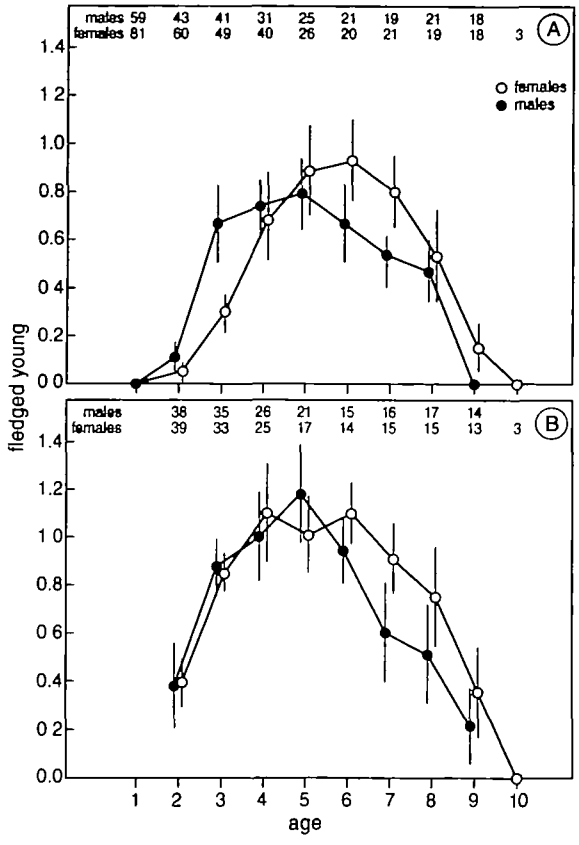

Figure 1
(A) Age-specific reproduction of annual number of young fledged (± SE) by male and female Seychelles warblers, including breeders and non-breeders (males: $r^2 = .15$, $p < .001$, $n = 278$; females: $r^2 = .24$, $p < .001$, $n = 337$). (B) Age-specific reproduction of annual number of young fledged (± SE) by breeding males and females only (males: $r^2 = .14$, $p = .003$, $n = 182$; females: $r^2 = .14$, $p = .003$, $n = 174$). In both figures, data are for males and females of precisely known ages, and only one randomly selected age category for each bird was used (top figures are number of males and number of females).

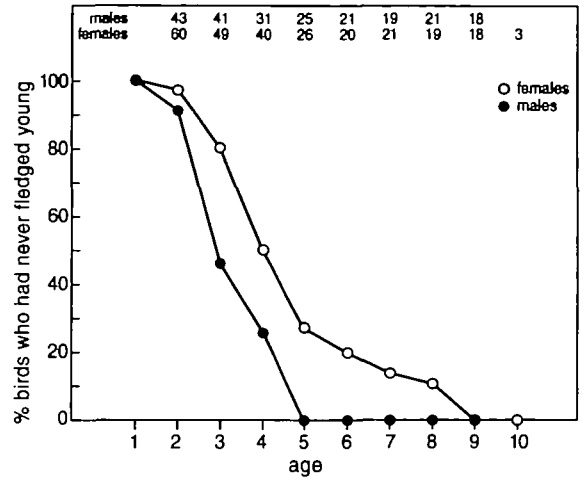

Figure 2
Percentage of Seychelles warblers that lived at least to the stated age that had never fledged young. In the analysis breeders and non-breeders were included. In each set of data a bird appears only once (top figures are number of males and number of females).

None of the females produced fledglings as 2-year-olds. Females did not increase their nest attempts as they grew older. However, 8-year-old birds built significantly fewer nests (Table 3). The proportion of nests containing a clutch, hatching, and fledging success increased from 2 to 4 years of age (Table 3). Consequently, there was a significant increase in production of hatched and fledged young from 2 to 4 years of age (Table 3). From 4 to 5 years of age, no further improvement in reproductive success was evident. From 5 to 7 years of age breeding performance declined significantly. A smaller proportion of nests contained a clutch, and hatching success was lower. As a consequence, fewer fledglings were produced (Table 3). Males decreased their nest attempts as they grew older (Table 3). However, hatching success increased from 2 to 3 years of age, and consequently there was an increase in the annual number of hatchlings and fledglings produced (Table 3). From 3 to 6 years of age, the annual number of fledglings produced remained the same, but from 6 to 7 years of age less fledglings were produced because of fewer nests containing a clutch (Table 3). Males and females did not change their foraging efficiency as they grew older (Table 3). On average, percentage of time spent foraging and foraging success of individual warblers were independent of age.

Compared with primiparous 3- and 4-year-old warblers (Table 1), multiparous 3- and 4-year-olds produced 1.3 and 1.4 more fledglings, respectively (Table 3). Overall, reproductive output varied with age and previous breeding experience of the bird, as indicated by a two-way ANOVA in which the effects of age and previous breeding experience were significant (age: $F_{1,82}=11.11$, $p = .001$; previous breeding experience: $F_{1,82} = 5.40$, $p = .022$; for multiparous birds only one randomly selected age category was taken).

DISCUSSION

Reproductive performance in relation to age at primiparity

Mean age of recruitment into the breeding population was 3.2 years for females and 3.0 years for males. This late age of first reproduction is related to the fact that the population on Cousin Island has remained stable since 1982 and the island is completely covered with territories (Komdeur, 1992, 1994b, in press a; Komdeur et al., 1995). On the islands of Aride (68 ha) and Cousine (26 ha) where the breeding populations are

Table 2
Combined effects of territory quality, group size, age of the bird, number of males and females in the group, year of study and sex of the bird on annual reproductive success of the Seychelles warbler (forward multiple regression)

Independent variable	F	Cumulative r^2	p
Number of fledged young			
Territory quality	63.72	0.164	<.001
Group size	9.09	0.186	.003
Sex of bird	4.71	0.198	.031
Age of bird	4.28	0.208	.039
(Age of bird)^2	58.50	0.330	<.001
(Territory quality)^2	8.50	0.347	.004
Number of females	0.73	0.349	.394
Number of males	0.11	0.347	.743
Year of study	0.01	0.347	.910

Data were pooled during 14 years of study (1981–1994), and only one randomly selected age category for each bird was used (n = 356 observations; 182 males and 174 females).

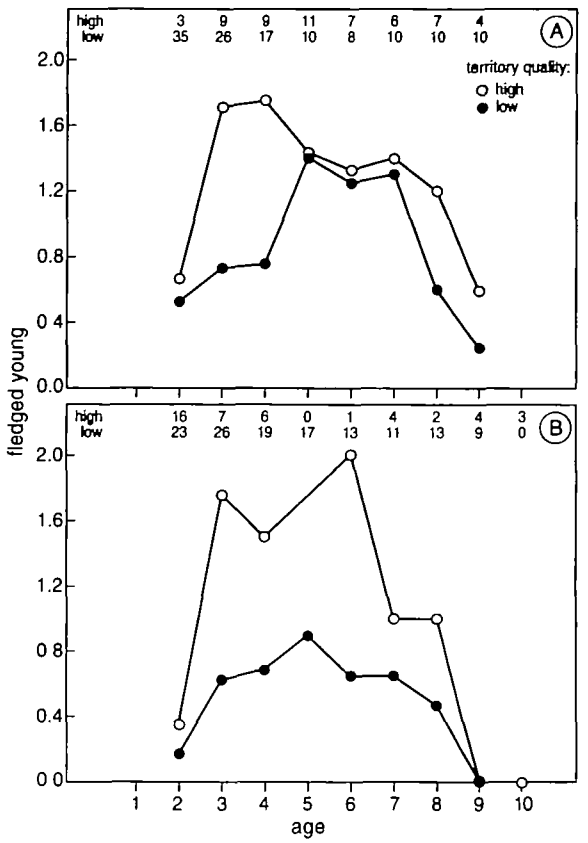

Figure 3
(A) Age-specific reproduction of annual number of young fledged by breeding male Seychelles warblers occupying low- or high-quality territories [$F(tq) = 12.22$, df = 1, $p < .001$; F (age) = 4.80, df = 7, $p < .001$; F ($tq \times$ age) = 0.65, df = 7, $p = 0.731$; $n = 182$]. (B) Age-specific reproduction of annual number of young fledged by breeding female Seychelles warblers occupying low- or high-quality territories [$F(tq) = 10.61$, df = 1, $p < .001$; F (age) = 5.93, df = 7, $p < .001$; F ($tq \times$ age) = 2.62, df = 6, $p < .025$; $n = 174$]. In both figures, data are pooled during 14 years of study (1981–1994), and data are for males and females of precisely known ages paired with an experienced partner. Only one randomly selected age category for each bird was used. Values presented are adjusted means calculated using analysis of variance in which the effect of helpers was controlled (top figures are number of males and number of females occupying high- or low-quality territories).

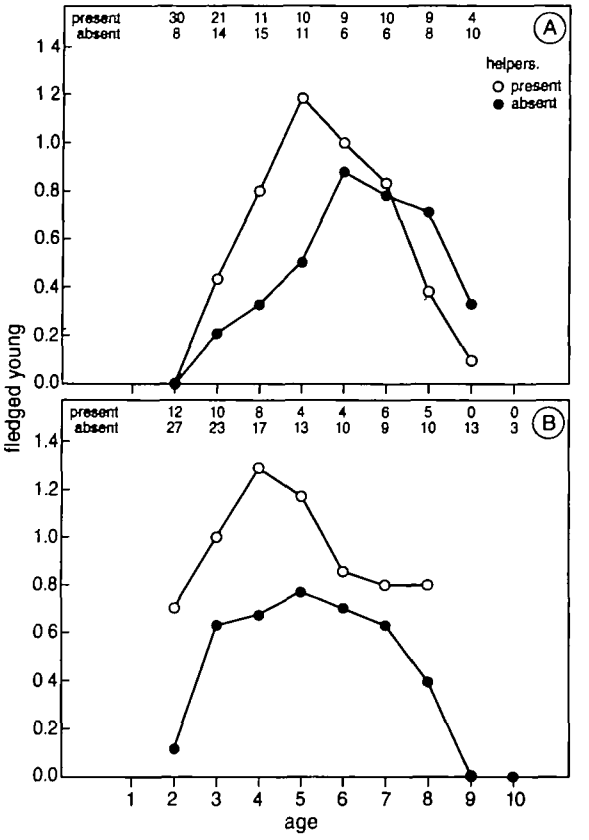

Figure 4
(A) Age-specific reproduction of annual number of young fledged by breeding male Seychelles warblers without or with presence of helpers [F(helper) = 4.06, df = 1, $p < .05$; F (age) = 4.57, df = 7, $P < .001$; F (helper $\times$ age) = 1.17, df = 7, $p = 0.322$; $n = 182$). (B) Age-specific reproduction of annual number of young fledged by breeding female Seychelles warblers without or with presence of helpers [F(helper) = 24.66, df = 1, $p < .001$; F (age) = 7.65, df = 6, $p < .001$; F (helper $\times$ age) = 2.63, df = 6, $p < .025$; $n = 174$]. In both figures, data are pooled during 14 years of study (1981–1994), and data are for males and females of precisely known ages paired with an experienced partner. Only one randomly selected age category for each bird was used. Values presented are adjusted means calculated using analysis of variance in which the effect of territory quality was controlled (top figures are number of males and number of females with or without presence of helpers).

still expanding after introductions in 1988 and 1990, respectively (Komdeur, 1994b, in press a; Komdeur et al., 1991), age of recruitment is significantly earlier and occurs before the birds reach 1 year of age, because breeding opportunities are available year-round (Komdeur, 1994b, in press a). In the present study on Cousin Island, I found evidence for variation in reproductive performance caused by age at primiparity (Table 1). Two-year-old female and male primiparae produced, respectively, no and few independent young, whereas the number of independent young produced by 3- and 4-year-old female and male primiparae was significantly higher (Table 1). The enhanced offspring production by older primiparae was attributed to higher probability of nests containing an egg in females, higher hatching success in both sexes, and to higher fledging success in females (Table 1). These results were not likely be confounded by individual foraging skills; for any age class of male and female primiparae, foraging success and percentage time spent foraging did not differ significantly (Table 1).

Reproductive performance in relation to age and breeding experience

Older Seychelles warblers produced significantly more fledglings than younger birds (Figures 3, 4, and 5; Tables 2 and 3). This is in accordance with observations in many other bird species (Clutton-Brock, 1988; Forslund and Larsson, 1992; Newton, 1989; Nol and Smith, 1987; Sæther, 1990). This pattern was consistent in different environments. Age-specific reproduction was observed for birds occupying low- and high-quality breeding territories (Figure 3) and for birds without or with helpers present (Figure 4). A closer examination, using longitudinal data, showed that females and males had higher hatching success and produced more hatchlings and fledglings as they became older (Table 3). The enhanced reproductive success is not caused by differential survival, because the age-related changes in reproductive success were based on breeding individuals with both high and low reproductive success that survived to at least 8 years. Instead, an increase in reproductive success with age could be explained

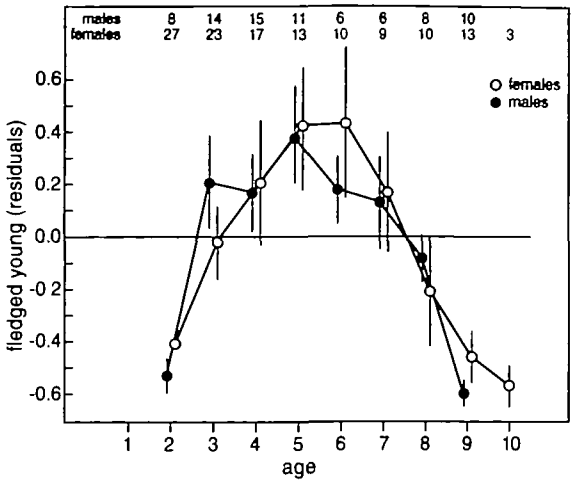

Figure 5
Age-specific reproduction of annual number of young fledged by breeding male and female Seychelles warblers pooled during 14 years of study (1981–1994). Data are for males and females of precisely known ages paired with an experienced partner. Data were standardized for group size effects by considering breeding pairs only. Only one randomly selected age category for each bird was used. Values presented are adjusted means (residuals ± SE) calculated using analysis of variance in which the effects of territory quality was controlled (males: annual number of fledged young = $0.245 * \text{age} - 0.004 * \text{age}^3 - 0.472$, $r^2 = .19$, $n = 81$, $p < .001$, m = number of males; females: annual number of fledged young = $0.967 * \text{age} - 0.166 * \text{age}^2 + 0.007\ \text{age}^3 - 1.287$, $r^2 = .30$, $n = 122$, $p < .001$, f = number of females). The curves described by these models provided a good fit to the data because the addition of other terms did not add significantly to the fit (males: $p > .075$; females: $p > .373$) (top figures are number of males and number of females).

by increased reproductive effort (Charlesworth, 1980; Gadgil and Bossert, 1970; Pianka and Parker, 1975; Williams, 1966) and/or improved skills with age (Curio, 1983; Nol and Smith, 1987; Partridge, 1989). Individuals should increase their reproductive effort with age as a response to decreasing residual reproductive value caused by decreasing life expectancy as they become older. However, this study showed that it is unlikely that this factor could contribute significantly to the observed increase. Annual production of fledglings was similar for primiparous and multiparous warblers (which had bred in previous years) of the same age, with same life expectancy, and occupying territories with similar amount of resources available for reproduction (Tables 1 and 3). Therefore, I suggest that improved skill with age is the primary factor behind the age-related increase in reproductive success in the Seychelles warbler.

Improved foraging skills has been frequently suggested for increased reproductive success with age early in life (Burger, 1988; Desrochers, 1992; Forslund and Pärt, 1995; Lack, 1968; Newton, 1989; Pyle et al., 1991). An increase in foraging efficiency presumably affects the amount of energy that can be allocated to reproduction without incurring additional survival costs. However, in the Seychelles warbler breeding performance did not improve with age as a consequence of improved foraging skills (Table 3). The percentage of time spent foraging and foraging success of individual warblers breeding on given quality territories seemed to be independent of age (Table 3). The reason for the observed increase in reproductive success with age is determined by the bird's experience with either helping or breeding (Komdeur, 1996). In their first year of breeding, reproductive performance of inexperienced warblers with neither helping nor breeding experience was significantly lower than that of warblers of the same age with either previous helping or breeding experience. Reproductive performance was as similar for primiparae with helping experience as for birds with breeding experience. Female primiparae with helping experience or females with breeding experience built better nests, had a higher probability of laying a clutch, and spent more time incubating than inexperienced females. Better nests prevent the egg from being destroyed by heavy rain and gusty wind. Increased incubation prevents the egg from chilling and retardation and possibly death of the embryo (Nelson, 1966), resulting in a higher hatching success in the Seychelles warbler (Komdeur, 1994a). Male primiparae with helping experience or males with breeding experience guarded the clutch better than inexperienced males, leading to reduced egg predation by Seychelles fodies and skinks (Komdeur, 1996). This resulted in a higher hatching success (Komdeur, 1994a, 1996). The effect of helping or breeding experience on breeding performance was experimentally tested by translocations of even-aged birds with different experiences to suitable unoccupied islands, where birds started breeding immediately in high-quality territories (Komdeur, in press a). Birds with helping experience that were paired with an experienced partner produced their first fledgling as fast as experienced breeders and significantly faster than inexperienced birds paired with an experienced partner. Breeding performance did not improve with experience after the first successful breeding attempt. These results were not confounded by individual foraging skills; inexperienced birds were as efficient in foraging as birds with helping or breeding experience of the same age (Komdeur, 1996).

Senescence effects on reproductive success in the Seychelles warbler began to occur from age 6 for both sexes (Figure 5, Table 3). Williams proposed that the evolution of senescence could be understood in terms of age-specific pleiotropic gene action, where a mutation increases fitness early in life at the expense of reducing it later on (Williams, 1957). A pleiotropic gene action would involve an initial genetic effect, for example a cost of reproduction, where an increase in reproductive rate reduces future fecundity that generates senescence (Partridge, 1987; Williams, 1957). In the Seychelles warbler, females did not increase their nest attempts as they grew older, but they produced fewer nests with clutch, and their eggs had lower hatching success (Table 3). This was probably not because of a decline in incubation efficiency. Although the same individuals spent the same percentage time incubating at 4–5 years of age as at 6–7 years of age (mean % incubation: 41.0% ± 6.3 SD versus 45.2% ± 5.5 SD; $n = 13$, Wilcoxon test: $Z = 1.65$, $p = .10$), the lower hatching success could be caused by a lower incubation efficiency (warming and turning the eggs) or by a larger proportion of eggs being infertile. Unfortunately I have not been able to check whether eggs were fertile, because of the high predation rate of unattended eggs. Fledging success, however, did not decrease in the oldest age groups; birds are still efficient at chick feeding. Empirical support for Williams' idea that costly reproduction accelerates senescence for fertility was provided by the study on the collared flycatcher (*Ficedula albicollis*; Gustafsson and Pärt, 1990). In this species, females with experimentally enlarged brood size laid smaller clutches later in life than those with a reduced or unmanipulated brood. This brood manipulation and the birds' decision about when to start breeding have mimicked the early genetic effect, and the subsequent drop in clutch size presumably would then be caused by ordinary physiological effects on the early effort.

Longitudinal data showed that until senescence, the annual nest-building attempts were the same for young and older Seychelles warblers, but reproductive success of older birds was

Table 3

Within-individual, age-related changes in reproductive success (SE), and foraging efficiency (SE) in Seychelles warblers, paired with the same experienced partner and occupying the same low quality breeding territories from 2 to 8 years of age

	Age							
	2	3	4	5	6	7	8	p
Females (17)								
Nest attempts	1.18 (0.25)	1.41 (0.17)	1.29 (0.11)	1.18 (0.10)	0.94 (0.10)	0.77 (0.14)	0.71 (0.14)**	.008
Proportion with clutch	0.30	0.79	1.00	1.00	0.81	0.77	0.67	
Nests with clutch	0.35 (0.15)***	1.12 (0.19)	1.29 (0.11)**	1.18 (0.10)***	0.77 (0.14)**	0.59 (0.15)	0.47 (0.13)	.01
Hatchlings/egg	0.17	0.74	0.96	0.95	0.54	0.50	0.63	
Nestlings	0.06 (0.06)*	0.82 (0.18)*	1.24 (0.14)**	1.12 (0.12)***	0.41 (0.12)**	0.29 (0.11)**	0.29 (0.11)**	.001
Fledglings/ hatched egg	0.00	0.86	0.86	0.95	0.71	1.00	0.00	
Fledged young	0.00 (0.00)***	0.71 (0.14)***	1.06 (0.14)***	1.06 (0.14)**	0.29 (0.11)***	0.29 (0.11)*	0.00 (0.00)***	.001
% Foraging	84.4 (12.6)	85.3 (11.3)	84.4 (10.7)	83.8 (11.8)	85.4 (11.6)	87.9 (4.9)	90.1 (5.7)	NS
Foraging success	2.19 (0.56)	2.45 (0.91)	2.68 (0.81)	2.41 (0.67)	2.09 (0.87)	2.43 (0.81)	2.61 (0.87)	NS
Territory quality	8.34 (2.83)	7.63 (3.20)	7.63 (2.38)	5.92 (1.96)	6.73 (2.97)	8.32 (3.12)	7.08 (4.03)	NS
Males (15)								
Nest attempts	1.00 (0.22)*	0.93 (0.15)*	1.20 (0.18)*	0.87 (0.19)*	0.73 (0.12)	0.67 (0.16)	0.33 (0.13)	.004
Proportion with clutch	0.73	0.86	0.94	1.00	1.00	0.70	0.00	
Nests with clutch	0.73 (0.18)***	0.80 (0.15)***	1.13 (0.17)**	0.87 (0.19)**	0.73 (0.12)	0.47 (0.13)	0.00 (0.00)*	.001
Hatchlings/egg	0.46	0.83	0.94	0.92	0.64	0.57	0.00	
Nestlings	0.33 (0.13)**	0.67 (0.13)**	1.07 (0.18)***	0.80 (0.18)**	0.47 (0.13)	0.27 (0.12)	0.00 (0.00)*	.001
Fledglings/ hatched egg	0.60	0.90	0.94	1.00	1.00	1.00	0.00	
Fledged young	0.20 (0.11)**	0.60 (0.13)	1.00 (0.20)**	0.80 (0.18)**	0.47 (0 13)	0.27 (0.12)	0.00 (0.00)**	.001
% Foraging	86.9 (11.4)	86.2 (10.4)	80.6 (12.8)	87.1 (10.9)	83.3 (10.2)	88.9 (5.5)	85.3 (11.4)	NS
Foraging success	2.34 (0.68)	2.22 (0.43)	2.65 (0.87)	2.33 (0.87)	2.27 (0.91)	1.97 (0.42)	2.51 (0.61)	NS
Territory quality	7.43 (3.21)	6.43 (2.83)	8.33 (4.21)	7.43 (3.92)	8.54 (3.92)	7.32 (2.87)	6.34 (4.10)	NS

Probability levels derived from a multivariate analysis of variance designed for repeated measures (MANOVA); * $p < .05$, ** $p < .025$, *** $p < .001$.

significantly higher (Table 3). This was not because of an increase in quality of breeding territory or a decrease in abundance of nest predators. The quality of breeding territories remained constant between years (Table 3; Komdeur, in press b), and the abundance of predators did not change over time (Brooke and Houston, 1983; Komdeur, 1991, 1994b; Owen, 1986). As warblers had similar access to food before reproduction and similar foraging efficiency (Table 3), the reason for the low reproductive success in younger warblers has not to be sought in differences in environment, but in differences in the bird's ability to breed successfully.

Costs and benefits of early or late breeding

According to life-history theory, individuals should begin to reproduce when the net benefits are greater than the net benefits of delaying reproduction (Promislow and Harvey, 1990; Stearns, 1992). Early reproduction can be beneficial if it reduces the probability of an individual dying before any offspring have been produced or increases the number of offspring produced in an individual's lifetime, but it may be costly if survival, fecundity or offspring survival are reduced (Harvey and Zammuto, 1985; Stearns, 1992). In the Seychelles warbler early breeding on a given quality territory is better than delayed breeding: (1) For both sexes, the reproductive pay-off was independent of age. The proportion of primiparous birds that fledge young the following season was independent of age at primiparity (Table 1); (2) in both sexes, 2- and 3-year-old primiparae produced significantly more fledglings over their estimated lifetime than 4-year-old primiparae (Table 1). However, the fraction of older birds that had never fledged young of their own was quite large (Figure 2). Most birds have not been able to fill breeding vacancies, because of a shortage of breeding territories (Komdeur, 1992; Komdeur et al., 1995). Most birds delaying breeding become helpers. By helping birds gain indirect benefits through increased production of the helper's non-descendent kin (Komdeur, 1994c). Another reason for helping could be to gain helping experience, which may translate into improved reproductive success when a helper becomes a breeder (Emlen and Wrege, 1989; Koenig and Mumme, 1990). The translocations of even-aged Seychelles warblers with different experiences to unoccupied islands, showed that birds with helping experience produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds (Komdeur, 1996). In this experiment breeding experience was not associated with individual quality. On the new islands all pairs with different previous experiences started breeding within 2 to 3 weeks after pair formation (Komdeur, 1996). Also, primiparous birds with helping experience have greater lifetime reproductive success than inexperienced primiparae of the same age (Komdeur, 1996). In the Seychelles warbler helping behavior has also been selected for in the context of gaining helping experience, which translates into improved lifetime reproductive success when a helper becomes a breeder.

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